

Prairie Grasses as Hosts of the Northern Corn Rootworm (Coleoptera: Chrysomelidae)

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ABSTRACT We evaluated 27 prairie grass species thought to be among those dominant 200 yr ago in the northern midwest as larval hosts of the northern corn rootworm, *Diabrotica barberi* Smith and Lawrence. Maize (*Zea mays* L.), spring wheat (*Triticum aestivum* L.), and grain sorghum (*Sorghum bicolor* L.) were included as controls for a total of 30 species. Twenty pots of each species were planted in a randomized complete block design. Each pot was infested 5 wk later with 20 neonate northern corn rootworm larvae. Two pots within each species and block were assigned an extraction date of 7 or 14 d after infestation. The remaining two pots from each block were used to monitor adult emergence. The percentage of larvae recovered, change in larval head capsule width, and change in average dry weights varied significantly among the grass species. The highest percentage of larvae was recovered from slender wheatgrass, *Elymus trachycaulus* (Link), and this was significantly greater than the percentage recovered from all other species including maize for the 14-d sample date. Several additional species were also relatively good hosts, in that the percentage of larvae recovered from these species was not significantly different from maize. The average dry weight of larvae recovered was significantly greater for larvae recovered from maize than for larvae recovered from all other species except slender wheatgrass, when the two samples dates were combined. Overall, adults were produced from only 6 of the 28 species evaluated, and no analysis was performed because of the low numbers. The results of this study are discussed in relation to the potential of alternate hosts of northern corn rootworm to serve as a bridge to survival on transgenic maize.

KEY WORDS prairie grasses, alternate hosts, resistance management, *Diabrotica barberi*

The northern corn rootworm, *Diabrotica barberi* Smith and Lawrence, is one of the most severe pests of maize, *Zea mays* L., in the Corn Belt of the United States and is currently the dominant rootworm species in parts of Minnesota, South Dakota, and Iowa. Damage is caused when larvae feed directly on the roots. Together with the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, losses in terms of control costs and yield reduction are estimated at \$1 billion annually (Metcalf 1986).

Management tactics such as crop rotation and application of soil insecticides have been fairly effective, but the development of resistance to crop rotation through extended diapause (Krysan et al. 1986) has led to economic damage in rotated maize in many

areas. Additional control tactics, such as the use of transgenic maize that express a specific endotoxin(s) from the bacterium *Bacillus thuringiensis* Berliner (*Bt*), have been developed by several seed companies to control damage from the northern and western corn rootworm larvae (Moellenbeck et al. 2001, Ellis et al. 2002, Vaughn et al. 2005). However, the U.S. Environmental Protection Agency has mandated that a resistance management plan be developed before registration of *Bt* crops. Efforts to optimize insect resistance management plans of northern and western corn rootworms to transgenic maize have renewed interest in the basic biology of these insects because many parameters required by models used to evaluate resistance management plans are unknown (Onstad et al. 2001, Storer 2003, Crowder and Onstad 2005, Mitchell and Onstad 2005, Crowder et al. 2005). According to the literature database Agricola (U.S. National Agricultural Library), the number of corn rootworm papers published in 2005 was more than in all but 2 of the previous 40 yr and was nearly double the number that had been published for the average of the previous 10 yr. Many of these studies were stimulated by the current demand for additional information on the basic biology of these important pests.

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Table 1. List of prairie grasses screened as alternate hosts of northern corn rootworm larvae

Taxonomy of species evaluated ^a	Economic importance	Source
Family Poaceae		
Subfamily Panicoideae		
Tribe Andropogoneae		
Maize, <i>Zea mays</i> L.	Crop	DKC60-15; Dekalb, St. Louis, MO
Sorghum, <i>Sorghum bicolor</i> L.	Crop	84C62; Pioneer Hi-Bred, Johnston, IA
Indian grass, <i>Sorghastrum nutans</i> L.	Forage/ornamental	Western Native Seed, Coaldale, CO
Big bluestem, <i>Andropogon gerardii</i> Vitman	Forage	Western Native Seed, Coaldale, CO
Little bluestem, <i>Schizachyrium scoparium</i> Michaux	Forage/wildlife	Western Native Seed, Coaldale, CO
Tribe Paniceae		
Witch grass, <i>Panicum capillare</i> L.	Forage/ornamental	Valley Seed Service, Fresno, CA
Subfamily Pooideae		
Tribe Triticeae		
Western wheatgrass, <i>Pascopyrum smithii</i> (Rydb.) Löve	Forage	Western Native Seed, Coaldale, CO
Pubescent wheatgrass, <i>Elytrigia intermedia</i> (Host) Nevski	Forage/not native	Western Native Seed, Coaldale, CO
Canada wild rye, <i>Elymus canadensis</i> L.	Forage	Western Native Seed, Coaldale, CO
Slender wheatgrass, <i>Elymus trachycaulus</i> (Link) Gould	Forage	Western Native Seed, Coaldale, CO
Wheat (Spring), <i>Triticum aestivum</i> L.	Crop	Bulk mix; MFA, Columbia, MO
Bottlebrush grass, <i>Elymus hystrix</i> L.	Erosion	Ernst Conservation Seeds, Meadville, PA
Tribe Stipeae		
Green needle grass, <i>Nassella viridula</i> (Trin.) Barkworth	Forage	Western Native Seed, Coaldale, CO
Needle-and-thread grass, <i>Hesperostipa comata</i> (Trin. and Rupr.)	Forage	Western Native Seed, Coaldale, CO
Tribe Aveneae		
Redtop, <i>Agrostis gigantea</i> Roth	Forage/not native	Seeds Trust, Cornville, AZ
Reed Canary grass, <i>Phalaris arundinacea</i> L.	Forage	IAmShaman, Chicago, IL
Prairie june grass, <i>Koeleria macrantha</i> (Ledeb.) Schult.	Turf	Western Native Seed, Coaldale, CO
Tribe Bromeae		
Smooth brome, <i>Bromus inermis</i> Leyss	Forage	Sharp Brothers Seed Co., Clinton MO
Subfamily Chloridoideae		
Tribe Cynodonteae		
Side-oats grama, <i>Bouteloua curtipendula</i> (Michaux)	Forage	Western Native Seed, Coaldale, CO
Buffalo grass, <i>Bouteloua dactyloides</i> (Nutt.)	Lawn/forage	Western Native Seed, Coaldale, CO
Prairie cordgrass, <i>Spartina pectinata</i> Link	Erosion/ornamental	Western Native Seed, Coaldale, CO
Galleta, <i>Pleuraphis jamesii</i> Torr.	Forage	Western Native Seed, Coaldale, CO
Blue grama <i>Bouteloua gracilis</i> (Kunth) Lag. Ex Griffiths	Forage	Sharp Brothers Seed Co., Clinton MO
Tribe Eragrostideae		
Prairie sandreed, <i>Calamovilfa longifolia</i> (Hook.) Scribn.	Forage	Western Native Seed, Coaldale, CO
Prairie dropseed, <i>Sporobolus heterolepis</i> (Gray)	Forage	Western Native Seed, Coaldale, CO
Ring grass, <i>Muhlenbergia torreyi</i> (Kunth) Hitchc. Ex Bush	Ornamental	Plants of the Southwest, Sante Fe, NM
Tall dropseed, <i>Sporobolus compositus</i> (Poir.) Merr.	Forage/ornamental	Western Native Seed, Coaldale, CO
Sand dropseed, <i>Sporobolus cryptandrus</i> (Torr.) Gray	Forage/wildlife	Western Native Seed, Coaldale, CO
Sand lovegrass, <i>Eragrostis trichodes</i> (Nutt.) Wood	Forage	V & J Seed Farm, Woodstock, IL
Subfamily Arundinoideae		
Tribe Aristideae		
Purple threeawn, <i>Aristida purpurea</i> Nutt.	Ornamental	Western Native Seed, Coaldale, CO

^a According to the Germplasm Resources Information Network (GRIN), <http://www.ars-grin.gov/npgs/>.

The historical range of northern corn rootworm likely predates the introduction of maize into the region by Native Americans and colonizing farmers of European decent (Weatherwax 1954, Galinat 1977, Branson and Krysan 1981). It is possible that the northern corn rootworm used maize planted by native Americans, but the pest was not noted in the literature until large monocultures of continuous maize were grown in their native range in the 1880s (Webster 1896). Northern corn rootworm larvae likely primarily used unknown host plants before this time (Webster 1896, Branson and Krysan 1981, Krysan and Smith 1987). Currently there is no information on the original host(s) of the northern corn rootworm, other than it can develop on a number of grass species (Branson and Ortman 1967a, 1971, Oyediran et al. 2004b). The objective of this experiment was to evaluate the dominant prairie grasses that were present in the original range of the northern corn rootworm to see which best support larval development.

Materials and Methods

Plants, Insects, and Experimental Design. The experiment was conducted in a greenhouse in 2005. Twenty-seven prairie grass species, along with maize, sorghum (*Sorghum bicolor* L.), and spring wheat (*Triticum aestivum* L.) as checks, were evaluated for their suitability as larval hosts of the northern corn rootworm. The species chosen were among native species thought to dominate portions of the original range of the northern corn rootworm (Weaver and Albertson 1956, Schumacher and Derschied 1975, Branson and Krysan 1981). The seed source for each species was documented (Table 1). Before planting the full trial, 5 ml of seed of each species was planted in pots and soil described below. After 3 wk, each species was visually rated for fullness of stand. Final seed quantities used in the trial were adjusted up or down from 5 ml based on what was seen in the initial planting in hopes of providing as equal amount of root

tissue as possible. Seeds were planted in pots containing a 2:1 mixture of autoclaved soil:peat-based growing medium (Promix; Premier Horticulture LTEE, Québec, Canada). Drainage openings in the pots were fitted with a fine (114 μm /opening) stainless steel mesh (TWP, Berkeley, CA) to prevent larval escape (Clark and Hibbard 2004). The experimental design was a randomized completed block with a split-plot arrangement of treatments. The experiment evaluated survival and growth parameters among and within species over time. The main plot was plant species and the subplot was sample time/type. Because this was as a greenhouse experiment, the blocks were portions of the same greenhouse with slightly different lighting and air movement.

Twenty pots (ten 3.8 liter and ten 19 liter) of each test species were planted in a randomized complete block design with five blocks containing two pots of each size with each plant species. The two 3.8-liter pots within each block (=replication) were randomly assigned one of two sample dates for larval extraction. The remaining two pots from each block were used to monitor adult emergence. Five weeks after planting, each pot was infested with 20 neonate northern corn rootworm larvae (<24 h old) by gently transferring newly hatched larvae with a moistened fine nylon paintbrush into a hole (1 cm by 3 cm deep) that was dug in each pot. After infestation, each hole was gently covered with excess soil. A 14:10 (L:D) photoperiod was maintained with 1,000-W sodium lights (GE Lighting, Cleveland, OH). Temperature was maintained at $\approx 25^\circ\text{C}$. A temperature recorder was available during almost all of the experiment, and temperatures remained at a daily average of $25 \pm 2^\circ\text{C}$. The northern corn rootworm colony used for this study was maintained at the USDA-ARS facility in Brookings, SD, since 1996. There has been approximately one generation per year from this colony. The insects evaluated in this study represent the ninth generation of laboratory production. Rearing methods of Jackson (1986) were modified to include a more "cloddy" (0.5 cm diameter) oviposition substrate than the soil than is typically used for the western corn rootworm (soil that has been through a 70-mesh or 20- μm sieve for ease of egg recovery).

Larval Growth and Development. Seven and 14 d after infestation, the contents (soil mixture, roots, and larvae) of pots randomly assigned for larval recovery at that time were individually placed in Tullgren funnels equipped with a 60-W light bulb (Wal-Mart Co.) for the extraction of larvae. Collection jars containing water were placed under the funnels and checked daily for larvae for 4 d. Larvae recovered were counted and individually transferred to scintillation vials containing 95% ethanol. The head capsule width of each larva was measured using an ocular micrometer (10 \times /21; Wild Co., Heerbrugg, Switzerland) mounted on a microscope (M3Z; Wild Co.). The average head capsule width of the population of neonate larvae used to infest pots was 0.22 ± 0.01 mm. The change in larval head capsule width was calculated by subtracting 0.22 mm from the measured head capsule

width of the recovered larvae in question. When no larvae were recovered from a particular replication, it was assumed that the larvae did not grow, so the change in head capsule width for the replicate was considered zero. Dry weights of the larvae were determined using an analytical scale (ER-182A; A & D Co., Tokyo, Japan) after placing the larvae in a desiccating oven (Thelco model 16; GCA/Precision Scientific Co., Chicago, IL) at 80°C for 48 h. For dry weight, the change in weight was calculated by subtracting 0.0099 mg (the average initial dry weight of 154 neonate northern corn rootworm larvae) from the average dry weight of larvae recovered. When no larvae were recovered from a particular pot, the change in dry weight was considered zero.

Beetle Emergence. On the 28th day after infestation, the vegetation from the two 19-liter plastic pots was cut close to the soil level, and the pots were covered with a mesh to prevent beetle escape. Each pot was checked a minimum of twice per week for adult emergence. All the adults collected were stored in 95% ethanol. The adults were identified to sex, and the pronotum width and dry weight were measured as described earlier.

Statistical Analysis. The data were analyzed using PROC MIXED (SAS Institute 1990) as a randomized complete block split-plot in space outlined in Steel and Torrie (1980). A separate analysis was done for percent larval recovery, change in larval head capsule widths, and change in average dry weight of larvae. Because the treatments were arranged as a 30 by 2 (plant species \times sample date) factorial, the linear statistical model contained the main plot effect of plant species, the subplot effects of sample date, and their interaction. Replications \times plant species served as the denominator of F for testing the effects of plant species. The residual mean square served as the denominator of F for all other effects. Beyond the standard analysis of variance (ANOVA), we preplanned to compare plant species within sample dates and sample dates within plant species. This was done with the LSMEAN output from PROC MIXED (least significant difference [LSD] technique). Although untransformed data are shown in the tables, head capsule width and dry weight data were transformed by square root ($x + 0.5$) for analyses to meet the assumptions of equal variance. Percentage recovery data were converted by the arcsine (square root $x/100$). Because of the low numbers of adults recovered, no analysis was done on adult emergence data.

Results

Larval Recovery. Percent recovery of northern corn rootworm larvae from root masses placed in Tullgren funnels was significantly different among the species evaluated ($F = 7.03$; $\text{df} = 29, 116$; $P < 0.0001$) and the sample day ($F = 7.38$; $\text{df} = 1, 120$; $P = 0.0076$). The interaction between species evaluated and sample day ($F = 0.91$; $\text{df} = 29, 120$; $P = 0.5956$) was not significant. The highest percentage of larvae recovered was from slender wheatgrass, *Elymus trachycaulus*

Table 2. Percentage of northern corn rootworm larvae recovered from Tullgren funnels (mean \pm SEM)

Host species	Days after infestation		Species main effect
	Day 7	Day 14	
Maize	14.67 \pm 6.02 aA	12.00 \pm 5.33 aB	13.33 \pm 3.82 A-C
Western wheatgrass	12.67 \pm 3.23 aA	18.67 \pm 7.64 aB	15.67 \pm 4.04 AB
Slender wheatgrass	12.00 \pm 4.90 bA	32.00 \pm 11.43 aA	22.00 \pm 6.74 A
Canada wildrye	6.67 \pm 4.22 bA-D	20.00 \pm 6.91 aB	13.33 \pm 4.42 A-C
Pubescent wheatgrass	5.33 \pm 3.09 bB-E	10.00 \pm 4.35 aBC	7.67 \pm 2.63 B-D
Green needlegrass	0.0 aE	0.0 aD	0.0 F
Needle-and-thread grass	1.33 \pm 1.33 aC-E	1.33 \pm 0.82 aCD	1.33 \pm 0.74 EF
Redtop	12.00 \pm 4.90 aAB	20.67 \pm 13.10 aB	16.33 \pm 6.75 AB
Prairie junegrass	0.0 aE	0.67 \pm 0.67 aD	0.33 \pm 0.33 F
Big bluestem	2.67 \pm 1.94 bC-E	10.00 \pm 5.16 aBC	6.33 \pm 2.87 C-E
Witch grass	0.67 \pm 0.67 aDE	1.33 \pm 0.82 aCD	1.00 \pm 0.51 EF
Indian grass	8.00 \pm 3.43 aA-D	8.00 \pm 3.09 aBC	8.00 \pm 2.18 B-D
Little bluestem	0.0 aE	2.00 \pm 1.33 aCD	1.00 \pm 0.71 EF
Side-oats grama	0.67 \pm 0.67 aDE	1.33 \pm 0.82 aCD	1.00 \pm 0.51 EF
Blue grama	6.00 \pm 6.00 aB-E	4.00 \pm 4.00 aCD	5.00 \pm 3.42 D-F
Buffalo grass	10.0 \pm 6.83 aA-C	12.00 \pm 8.86 aBC	11.00 \pm 5.28 B-D
Prairie sand reed	2.67 \pm 2.67 aC-E	0.67 \pm 0.67 aD	1.67 \pm 1.34 EF
Purple three-awn	0.0 aE	0.0 aD	0.0 F
Prairie dropseed	0.0 aE	0.0 aD	0.0 F
Tall dropseed	1.33 \pm 0.82 aC-E	2.67 \pm 2.67 aCD	2.00 \pm 1.33 EF
Sand dropseed	0.0 aE	0.0 aD	0.0 F
Sand lovegrass	0.0 aE	0.67 \pm 0.67 aD	0.33 \pm 0.33 F
Prairie cord grass	0.0 bE	10.00 \pm 5.06 aBC	5.00 \pm 2.91 D-F
Galleta	0.0 aE	2.00 \pm 2.00 aCD	1.00 \pm 1.00 EF
Ring grass	0.0 aE	3.33 \pm 3.33 aCD	1.67 \pm 1.67 EF
Bottlebrush grass	6.67 \pm 3.50 aA-D	7.33 \pm 2.87 aBC	7.00 \pm 2.13 B-D
Sorghum	0.0 aE	0.0 aD	0.0 F
Reed canary grass	0.0 aE	1.33 \pm 0.82 aCD	0.67 \pm 0.44 EF
Spring wheat	15.33 \pm 1.33 aA	10.00 \pm 5.58 aBC	12.67 \pm 2.85 BC
Smooth brome	0.67 \pm 0.67 aDE	0.0 aD	0.33 \pm 0.33 F
Sample date main effect	3.92 \pm 0.01 b	6.40 \pm 0.01 a	

Although untransformed data are shown, statistics were performed using arcsine (\sqrt{x}) transformed data. Significant differences ($\alpha = 0.05$) between species within a column are indicated by different uppercase letters. Significant differences between sample dates within treatments in a row are indicated by different lowercase letters. N = 5.

(Link), which was significantly greater than the percentage of larvae recovered from all other species including maize 14 d after infestation (Table 2). When sample dates were combined, the percentage of larvae recovered from slender wheatgrass, spring wheat, western wheatgrass, Canada wildrye, redtop, buffalo grass, pubescent wheatgrass, Indian grass, big bluestem, and bottlebrush grass was not significantly lower than the percentage of larvae recovered from maize (Table 2). No larvae were recovered from sorghum, green needlegrass, purple three awn, prairie dropseed, or sand dropseed on either sample date. Trends within sample dates were generally similar to the combined analysis, except for slender wheatgrass, Canada wildrye, pubescent wheatgrass, big bluestem, and prairie cordgrass, where the first sample date had a significantly lower percentage of larvae recovered than on the second sample date (Table 2).

Head Capsule Width of Larvae. The average change in head capsule width (HCW) of larvae (obtained by subtracting 0.22 mm, the HCW of neonate control larvae) from the prairie grasses varied significantly among species ($F = 6.30$; $df = 29,116$; $P < 0.0001$) and sampling dates ($F = 43.24$; $df = 1,120$; $P = 0.0001$). The interaction between grass species and sample date ($F = 1.45$; $df = 29,120$; $P = 0.0846$) was not significant.

The HCW of field-collected neonate northern corn rootworms ranged from 0.20 to 0.26 mm, whereas second and third instars ranged from 0.28 to 0.40 and 0.42 to 0.56 mm, respectively (Hammack et al. 2003). Centers of fitted normal curves describing frequency distributions of HCW for first, second, and third instars were 0.227, 0.331, and 0.479 mm (Hammack et al. 2003). On sample day 14, larvae recovered from most of the plant species were either second or third instars. When sample dates were combined, there was no significant difference between the HCW of larvae recovered from maize and the HCW of larvae recovered from slender wheatgrass, western wheatgrass, Canada wildrye, redtop, buffalo grass, pubescent wheatgrass, Indian grass, big bluestem, bottlebrush grass, spring wheat, and prairie cordgrass (Table 3).

Average Dry Weight of Larvae. Average change in dry weight (obtained by subtracting 0.0099 mg from each recovered larva) varied significantly among prairies grass species ($F = 6.45$; $df = 29,116$; $P < 0.0001$), sample dates ($F = 67.05$; $df = 1,120$; $P = 0.0001$), and the interaction between prairie grasses and sampling dates ($F = 3.35$; $df = 29,120$; $P < 0.0001$). The average dry weight generally increased over time for all species except spring wheat, tall dropseed, and smooth brome (Table 4). For larvae recovered 14 d after

Table 3. Average (mean \pm SEM) change in head capsule width of northern corn rootworm larvae recovered from Tullgren funnels from an initial head capsule width of 0.22 mm

Host species	Days after infestation		Species
	Day 7	Day 14	
Main effect			
Maize	0.06 \pm 0.03 bA-D	0.19 \pm 0.05 aAB	0.13 \pm 0.03 A-C
Western wheatgrass	0.12 \pm 0.03 aA	0.20 \pm 0.05 aAB	0.16 \pm 0.03 AB
Slender wheatgrass	0.09 \pm 0.03 bAB	0.26 \pm 0.02 aA	0.18 \pm 0.03 A
Canada wildrye	0.07 \pm 0.02 bA-D	0.20 \pm 0.05 aAB	0.13 \pm 0.03 A-C
Pubescent wheatgrass	0.07 \pm 0.04 bA-D	0.17 \pm 0.05 aB-D	0.12 \pm 0.04 A-C
Green needlegrass	0.0 aD ^a	0.0 aH ^a	0.0 F ^a
Needle-and-thread grass	0.02 \pm 0.02 aB-D	0.03 \pm 0.02 aGH	0.02 \pm 0.01 F
Redtop	0.05 \pm 0.02 bA-D	0.14 \pm 0.06 aB-E	0.10 \pm 0.03 CD
Prairie junegrass	0.0 aD ^a	0.04 \pm 0.04 aGH	0.02 \pm 0.02 F
Big bluestem	0.06 \pm 0.04 bA-D	0.15 \pm 0.06 aB-E	0.10 \pm 0.04 B-D
Witch grass	0.01 \pm 0.01 aCD	0.06 \pm 0.04 aE-H	0.03 \pm 0.02 EF
Indian grass	0.05 \pm 0.02 bA-D	0.18 \pm 0.05 aAB	0.12 \pm 0.03 A-C
Little bluestem	0.0 bD ^a	0.09 \pm 0.06 aC-G	0.05 \pm 0.03 D-F
Side-oats grama	0.02 \pm 0.02 aB-D	0.03 \pm 0.02 aGH	0.02 \pm 0.01 F
Blue grama	0.02 \pm 0.02 aB-D	0.04 \pm 0.04 aGH	0.03 \pm 0.02 F
Buffalo grass	0.07 \pm 0.03 bA-D	0.13 \pm 0.05 aB-F	0.10 \pm 0.03 B-D
Prairie sand reed	0.01 \pm 0.01 aCD	0.05 \pm 0.05 aF-H	0.03 \pm 0.02 F
Purple three-awn	0.0 aD ^a	0.0 aH ^a	0.0 F ^a
Prairie dropseed	0.0 aD ^a	0.0 aH ^a	0.0 F ^a
Tall dropseed	0.04 \pm 0.03 aA-D	0.03 \pm 0.03 aGH	0.03 \pm 0.02 EF
Sand dropseed	0.0 aD ^a	0.0 aH ^a	0.0 F ^a
Sand lovegrass	0.0 aD ^a	0.05 \pm 0.05 aGH	0.02 \pm 0.02 F
Prairie cord grass	0.0 bD ^a	0.19 \pm 0.05 aAB	0.09 \pm 0.04 C-E
Galleta	0.0 aD ^a	0.04 \pm 0.04 aGH	0.02 \pm 0.02 F
Ring grass	0.0 aD ^a	0.04 \pm 0.04 aGH	0.02 \pm 0.02 F
Bottlebrush grass	0.09 \pm 0.04 bA-C	0.18 \pm 0.05 aA-C	0.13 \pm 0.03 A-C
Sorghum	0.0 aD ^a	0.0 aH ^a	0.0 F ^a
Reed canary grass	0.0 aD ^a	0.05 \pm 0.05 aGH	0.02 \pm 0.02 F
Spring wheat	0.11 \pm 0.02 aA	0.08 \pm 0.04 aD-H	0.10 \pm 0.02 B-D
Smooth brome	0.0 aD ^a	0.0 aH ^a	0.0 F ^a
Sample date main effect	0.03 \pm 0.01 b	0.08 \pm 0.01 a	

Although untransformed data are shown, statistics were performed using square root ($x + 0.5$) transformed data.

Significant differences ($\alpha = 0.05$) between species within a column are indicated by different uppercase letters. Significant differences between sample dates within treatments in a row are indicated by different lowercase letters.

N = 5.

^a No larvae were recovered and head capsule widths are assumed the same as neonate larvae (0.22 mm).

infestation, the average weight of larvae recovered from maize was significantly greater than the average weight of larvae recovered from all other species. The average dry weight of larvae recovered from slender wheatgrass after 14 d was significantly greater than the average dry weight of those recovered from all other species except maize and Canada wildrye (Table 4).

Adult Recovery. Adult recovery was extremely low. Only six of the prairie grasses produced at least one adult. A total of five adults were recovered from maize: two from western wheatgrass and one from pubescent grass, Indian grass, side oats grama, buffalo grass, and prairie cordgrass.

Discussion

In this study, we attempted to evaluate the host potential of dominant prairie grass species found in the original range of the northern corn rootworm. Northern corn rootworm larvae fed on and developed on most of the prairie grass species evaluated. The only species from which northern corn rootworm larvae were not recovered was green needle grass, purple three awn, prairie dropseed, sand dropseed, and the negative control, sorghum. In the combined analyses,

the percentage of larvae recovered from 10 of the species was not significantly less than the percentage of larvae recovered from maize (Table 2). The change in HCW was also not significantly less than that of maize for these same 10 species (plus prairie cordgrass) in the combined analysis (Table 3). It is clear that northern corn rootworm larvae are capable of using many grass species as hosts for at least some larval development.

When evaluated as a whole, data from Branson and Ortman (1967b, 1970), Clark and Hibbard (2004), Oyediran et al. (2004a), Wilson and Hibbard (2004), and unpublished data of B.E.H. indicate that all of the grass species evaluated in the tribes Poeae (fescues and related grasses) and Bromaeae (brome grasses) are relatively poor hosts for the western corn rootworm. Basically all of the species of the tribe Triticeae (wheatgrasses, ryegrasses, and related species) are relatively good hosts for the western corn rootworm. The tribe Andropogoneae, to which maize belongs, contains some of the very best hosts (maize and other *Zea* spp.), as well as some of the few grass species that are non-hosts (*Sorghum* spp.) for the western corn rootworm. All other grass tribes for which several grass species have been evaluated for western corn rootworm de-

Table 4. Average mean change in dry weight (mg; mean \pm SEM) of northern corn rootworm larval recovered from Tullgren funnels from an initial weight of 0.0099 mg

Host species	Days after infestation		
	Day 7	Day 14	Species main effect
Maize	0.07 \pm 0.03 bA	0.70 \pm 0.23 aA	0.39 \pm 0.15 A
Western wheatgrass	0.07 \pm 0.02 bA	0.30 \pm 0.08 aC	0.20 \pm 0.05 B-D
Slender wheatgrass	0.07 \pm 0.03 bA	0.50 \pm 0.15 aB	0.29 \pm 0.10 AB
Canada wildrye	0.05 \pm 0.01 bA	0.34 \pm 0.09 aBC	0.21 \pm 0.06 BC
Pubescent wheatgrass	0.03 \pm 0.01 bA	0.25 \pm 0.10 aC-E	0.14 \pm 0.06 C-F
Green needle grass	0.0 aA	0.0 aI	0.0 H
Needle-and-thread grass	0.0 aA	0.02 \pm 0.01 aI	0.01 \pm 0.01 GH
Redtop	0.05 \pm 0.02 bA	0.20 \pm 0.09 aC-G	0.14 \pm 0.05 C-F
Prairie junegrass	0.0 aA	0.09 \pm 0.06 aF-I	0.04 \pm 0.04 F-H
Big bluestem	0.08 \pm 0.07 bA	0.33 \pm 0.14 aC	0.21 \pm 0.08 BC
Witch grass	0.01 \pm 0.01 aA	0.07 \pm 0.05 aG-I	0.04 \pm 0.03 F-H
Indian grass	0.03 \pm 0.01 bA	0.23 \pm 0.09 aC-E	0.13 \pm 0.05 C-F
Little bluestem	0.0 A	0.06 \pm 0.04 aHI	0.03 \pm 0.02 GH
Side-oats grama	0.01 \pm 0.01 aA	0.03 \pm 0.02 aI	0.03 \pm 0.01 GH
Blue grama	0.01 \pm 0.01 aA	0.03 \pm 0.03 aI	0.02 \pm 0.02 GH
Buffalo grass	0.02 \pm 0.01 bA	0.14 \pm 0.09 aD-H	0.09 \pm 0.05 E-H
Prairie sand reed	0.01 \pm 0.01 aA	0.03 \pm 0.03 aI	0.02 \pm 0.02 GH
Purple three-awn	0.0 aA	0.0 aI	0.0 H
Prairie dropseed	0.0 aA	0.0 aI	0.0 H
Tall dropseed	0.02 \pm 0.01 aA	0.02 \pm 0.02 aI	0.02 \pm 0.01 GH
Sand dropseed	0.0 aA	0.0 aI	0.0 H
Sand lovegrass	0.0 A	0.09 \pm 0.09 aF-I	0.05 \pm 0.05 F-H
Prairie cord grass	0.0 A	0.21 \pm 0.06 aC-F	0.11 \pm 0.05 C-G
Galleta	0.0 A	0.04 \pm 0.04 aI	0.02 \pm 0.02 GH
Ring grass	0.0 A	0.04 \pm 0.04 aI	0.02 \pm 0.02 GH
Bottlebrush grass	0.09 \pm 0.06 bA	0.27 \pm 0.08 aC D	0.19 \pm 0.06 B-E
Sorghum	0.0 A	0.0 I	0.0 H
Reed canary grass	0.0 A	0.03 \pm 0.03 aGH	0.01 \pm 0.01 GH
Spring wheat	0.08 \pm 0.02 aA	0.11 \pm 0.06 aE-I	0.10 \pm 0.03 D-H
Smooth brome	0.01 \pm 0.01 aA	0.0 I	0.01 \pm 0.01 H
Sample date main effect	0.02 \pm 0.01 b	0.14 \pm 0.01 a	

Although untransformed data are shown, statistics were performed using square root ($x + 0.5$) transformed data.

Significant differences ($\alpha = 0.05$) between species within a column are indicated by different uppercase letters. Significant differences between sample dates within treatments in a row are indicated by different lowercase letters.

N = 5.

velopment (Eragrostideae, Paniceae, Aveneae, and Stipeae) include both species that were relatively good hosts and species that are relatively poor hosts for the western corn rootworm. In this study, of the 10 species that were not significantly less than maize for percent larval recovery for the northern corn rootworm, all were also relatively good hosts for the western corn rootworm.

None of the studies done to date with either the northern corn rootworm or the western corn rootworm has documented which hosts other than maize are actually used by these insect pests in agroecosystems. Johnson et al. (1984) showed that maize plots with high foxtail (*Setaria* spp.) populations produced fewer western and northern corn rootworm adults than plots that were kept weed free. Ellsbury et al. (2005) showed that western corn rootworm time to adult emergence was delayed in the presence of foxtail populations within maize plots. Grassy weeds within corn fields can apparently influence rootworm populations, but these data do not tell us to what extent maize versus foxtail was actually being used as a host.

Larval recovery from maize from this experiment was only 14% on the best sample date (Table 3), whereas recovery of the western corn rootworm from

maize in several similar trials (Clark and Hibbard 2004, Oyediran et al. 2004a, Wilson and Hibbard 2004, B.E.H., unpublished data) ranged from 30 to 56% from maize for the best sample dates in a particular experiment. These studies used nearly identical methods at the same location as this study. Comparisons would seem to suggest one of two alternatives or a combination thereof. Either the western corn rootworm larvae have a wider host range than northern corn rootworm larvae under greenhouse conditions used or the northern corn rootworm is not amenable to testing under greenhouse conditions used. The results on maize would lend some support to the latter possibility. Unfortunately, any differences in the host range of the western and northern corn rootworm are also confounded by differences in the current ability of humans to rear the two species on maize. Although the USDA-ARS laboratory in Brookings, SD, has been rearing the northern corn rootworm since 1996, this species is notoriously difficult to rear. These data seem to indicate that the northern corn rootworm has a somewhat limited host range compared with the western corn rootworm, but it is possible that the northern corn rootworm is not amenable to greenhouse evaluation.

The northern corn rootworm is currently the dominant rootworm species in parts of Minnesota, South Dakota, and Iowa. It is common throughout much of its range, which extends from Colorado to the coast of New York and from southern Canada to the northern portions of Alabama, Georgia, and South Carolina (Krysan and Smith 1987). The historical range of the northern corn rootworm likely predates the introduction of maize into the region by Native Americans and colonizing farmers of European descent (Galinat 1977, Branson and Krysan 1981), with northern corn rootworm larvae using unknown host plants (Webster 1896, Branson and Krysan 1981, Krysan and Smith 1987). The widespread distribution of maize production in the United States makes it difficult to assess whether or not larvae of the northern corn rootworm currently use hosts other than maize. Anecdotal evidence such as individual northern corn rootworm beetles being found miles from any corn source (T.L.C., unpublished data) have led some corn rootworm entomologists to believe that northern corn rootworms are currently using hosts in addition to maize, but this has not yet been documented.

Although natural northern or western corn rootworm populations using hosts other than maize are not documented, the Mexican corn rootworm, *D. v. zeae* Krysan and Smith, has been documented to develop on other hosts. Branson et al. (1982) collected Mexican corn rootworm beetles in emergence traps placed over a mixture of four grass species: *Brachiaria plantaginea* (Link), *Eleusine indica* L., *Eragrostis indica* (Hornem.), and *Digitaria ciliaris* (Retz.). They also collected larvae and pupae from the grasses *B. plantaginea* and *Panicum hallii* Vasey and the sedge *Cyperus macrocephalus* Liebm. in Mexico. Other examples exist, suggesting that this was not an isolated incident. Krysan and Smith (1987) cited an example in Sutton County, TX, where the Mexican corn rootworm was found at a density of two beetles per plant in a maize field in its third year of production (the second generation of potential beetle production from maize), despite >250 km of isolation from any other maize production area. The quick establishment of an economically damaging population (Witkowski et al. 1986) despite isolation strongly suggested that alternate larval hosts may have maintained a Mexican corn rootworm population in that area as well.

The implications of our data for resistance management of rootworm-resistant transgenic maize remain unclear. Oyediran et al. (2005) documented that significantly more western corn rootworm adults emerged from a mixture of transgenic corn and weeds than from either the transgenic corn alone or the weeds alone in greenhouse trials. Most of the species evaluated in this study are not considered weeds and would not normally be found within maize fields. Storer (2003) modeled adaptation of corn rootworms to rootworm-resistant *Bt* maize. This model predicted that, if as few as 0.5 to 1% of the adults come from spatially well-distributed nonmaize hosts, the onset of resistance would be significantly delayed in a system with a poorly distributed 5% fixed location refuge,

although this delay is not significant under more conservative refuge deployment scenarios, such as the 20% refuge being required for the product that is currently registered (N. Storer, personal communication). Unfortunately, the poor emergence of the northern corn rootworm from maize in this trial makes it impossible to suggest whether or not it may be likely that 0.5% of the northern corn rootworm adults found in maize fields come from nonmaize sources.

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